

**BEHAVIORAL CONTRIBUTIONS TO SEPARATION AND SUBSEQUENT
MORTALITY OF DOLPHIN CALVES CHASED BY TUNA PURSE-SEINERS
IN THE EASTERN TROPICAL PACIFIC OCEAN**

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JULY 2002

ADMINISTRATIVE REPORT LJ-02-28

ABSTRACT

The observation that fewer nursing calves than lactating females tend to found killed in tuna purse-seine sets in the eastern Tropical Pacific Ocean (ETP) (Archer et al. 2001) implies that at least some calves become permanently separated from their mothers as a result of the chase procedure. The long-term dependence of dolphin calves on their mothers implies that at least some of these separated calves may subsequently die due to loss of their mother. Such unobserved mortality could be contributing to the apparent lack of recovery of the dolphin populations in the ETP. This report qualitatively examines behavioral characteristics that might contribute to calf separation during chase and subsequent unobserved mortality by relating observed chronologies of dolphin mother-calf relationships from birth through about two years of age, to activities involved in chase and encirclement during tuna purse seine sets in the ETP. Behavior of calves at all ages will likely focus on attempting to maintain close physical association with their mothers during times of stress (i.e., perceived threat of chase by tuna-seiners). Behavior of mothers during times of perceived threat appears likely to focus more on remaining associated with the rest of the adults in the school rather than remaining closely associated with their calves. Because stress reactions of dolphin schools involve increased swimming speed, the disparity between calves and mothers with respect to physical size and stamina may contribute significantly to likelihood of separation, especially for smaller calves, faster chase speeds and longer chase durations. Calves that do become separated from their mothers likely face increased risk of mortality due to predation and/or starvation, due to the behavioral propensity of calves for continuous acoustic signaling during separation (thus increasing risk of perception by predators) and due to the behavioral propensity of adult female dolphins to avoid adopting orphaned calves.

Both likelihood of separation and increased risk of mortality will apparently be greatest for the youngest calves and will likely decrease only slowly over the first two or three years after birth. Overall, it appears that likelihood of separation, and subsequent mortality of the calf if not reunited with its mother, is quite high during the first two years and at least moderately high through the third year after birth. Common behavioral characteristics of mothers and both physical and behavioral characteristics of calves strongly suggest that mother-calf pairs are quite likely to become separated during chase by tuna vessels and that calves which are not soon reunited with their mothers are quite likely to succumb to unobserved mortality due to predation or starvation. Behaviorally-mediated separation of mother and calves is likely contributing to the observed deficit of calves compared to lactating females in dolphin set kill as well as to subsequent unobserved mortalities. These unobserved mortalities would contribute to decreased growth of ETP dolphin stocks. This is important because even a relatively low unobserved kill of calves could lead to the stocks' apparent lack of recovery of ETP dolphin populations.

INTRODUCTION

Tuna purse-seiners in the eastern tropical Pacific Ocean catch schools of large yellowfin tuna by locating, chasing and encircling schools of dolphins (primarily the spotted dolphin *Stenella attenuata*) with which yellowfin tuna frequently associate in this area. Although the massive dolphin mortality that used to result from this fishing method prior to the early 1990's appears to have been largely eliminated (to less than 0.01% of current population level) concern remains that

the chase and encirclement procedure continues to cause significant set-related unobserved mortality, particularly of calves. Unobserved mortality of calves is indicated by an observed deficit of calves compared to the number of lactating females killed in single sets by tuna purse-seiners in the ETP (Archer et al. 2001). This deficit implies that those dolphins's calves become permanently separated from their mothers during chase. These calves presumably remain at large somewhere in the ocean and are likely subject to an increased risk of subsequent mortality due to predation and/or starvation, having been deprived of their mother's nutrition and protection. This is significant because even a relatively low unobserved mortality of calves (e.g., fewer than 1 calf per set (Archer et al. 2000) could lead to the apparent lack of recovery of the dolphin population since reported mortality fell to very low levels in the early 1990's. How and why dolphin mothers and calves become separated during chase and encirclement is currently unknown, but both behavioral and physiological factors are likely involved given the relatively helpless physiological state of newborn dolphins and the long developmental period during which they continue to be dependent upon the mother for nutrition, protection, and training, and emotional support.

The present study examines behavioral factors that might contribute to mother-calf separation during chase by tuna boats and to subsequent unobserved mortality of the calf. The study reviews and summarizes the existing literature on chronological development of mother-calf behavior in dolphins. Section I summarizes mother-calf behavior through year two in both captive and wild dolphins. Section II describes the tuna vessel chase and encirclement procedure. Section III discusses likely behavioral responses to chase, for the school as a whole, for mother dolphins, and finally for dolphin calves, with respect to how these behaviors may contribute to separation and subsequent mortality of dolphin calves. Section IV discusses the likelihood of successful adoption of orphaned dolphin calves in the ETP.

Although the species of dolphin chased and encircled most often by tuna purse-seiners in the ETP is the pantropical spotted dolphin (*Stenella attenuata*), almost all of the information presented in this report is derived from observations on captive and/or wild common bottlenose dolphins (*Tursiops truncatus*) and Indian Ocean bottlenose dolphins (*Tursiops aduncus*) because these are the species for which most information exists. However, the bottlenose information should be relevant to questions about mother-calf relationships in spotted dolphins because both spotted and bottlenose dolphins, in common with most other herd-forming dolphin species, have very similar patterns of morphological, physiological, and social development (e.g., Wells 1991, Norris et al. 1994, Connor 2000). In addition, much of the recent detailed information from wild bottlenose dolphins has been collected from *Tursiops aduncus* in Shark Bay, Australia. Unlike most bottlenose, which tend to be much larger than *Stenella attenuata* in the ETP, the *Tursiops aduncus* in Shark Bay are about the same size as *Stenella*. (i.e., about 180-220 cm total length as adults)¹.

An independent scientific peer review of this work was administered by the Center for Independent Experts located at the University of Miami. Responses to reviewer's comments can be found in the Appendix.

¹Dr. Janet Mann, pers. comm., October 2001, Georgetown University, Georgetown, MD, USA.

I: Chronology of Calf Development

The following sections summarize published information regarding mother and calf behavior during successive stages in development beginning with the day of birth and continuing through periods of increasing length from the first week, the first three months, the second three months, the first two years, and after two years. Developments in swimming activity/position(s), respiration, suckling, separations/associations and acoustics are discussed separately in each section. Each section concludes with a brief summary of mother-calf behaviors during that period. The amount of existing information available for each section and age varies widely in the available literature so that some sections are extensive while others are rather scant. The first three sections, summarizing changes during the first three months, are the most extensive because this is the period during which morphology, physiology, and behavior change most dramatically.

Birth - Day 1: Numerous descriptions exist of dolphin births and subsequent mother-calf behavior. Most involve observations of births in captivity (McBride and Kritzler 1951, Essapian 1953, Tavolga and Essapian 1957, Taylor et al. 1972, Gurevich 1977, Reid et al. 1995) but a few include observations from wild dolphins (e.g., Wells 1991). The process seems to be similar in both wild and captive situations although individual differences can exist in the particulars of such activities as duration of parturition, initiation of suckling by the calf, and so forth (Tavolga and Essapian 1957, Chirigin 1987, Reid et al. 1995, Mann 1997, Triossi et al. 1998, Gubbins et al. 1999, Mann and Smuts 1999, Meury 1999).

Swimming Activity/Position(day 1): The birth process reportedly takes about half an hour for healthy births (e.g., Sweeney 1977). The neonate dolphin reportedly emerges tail first and surfaces immediately to take its first breath, sometimes with but more often without direct assistance from the mother ((McBride and Kritzler 1951, Essapian 1953, Tavolga and Essapian 1957). This initial surfacing is likely facilitated by the fact that calves tend to be positively buoyant with blubber mass exceeding muscle mass (Cockcroft and Ross 1990, Edwards 1993). The placenta is usually expelled later, within an hour or so, with accompanying blood and tissues staining the surrounding waters.

Although the initial respiration tends to be accomplished by the calf alone, under normal (i.e., non-chase) conditions subsequent respirations as well as most swimming activity tends to be closely synchronized between the mother and her newborn for at least the first few days (e.g., Mann and Smuts 1999). This is likely because at birth and for at least several hours thereafter dolphin calves have relatively little capacity for controlled swimming and could not independently maintain a close association with the mother except at very slow swim speeds, if then.

The importance of close synchrony between movements of mother and neonate following birth is illustrated by observations in captive situations. Newborn dolphin calves reportedly have such poor control of directional responses following birth that they tend to collide with tank walls as well as inadvertently beaching themselves in shallow areas if not under the mother's control (e.g., Taylor et al. 1972, Reid et al. 1995). Neonates reportedly also have limited ability to maintain an even keel just after birth (Cockcroft and Ross 1990) and tend to be clumsy and inefficient in their attempts at surfacing to breathe (e.g., Mann and Smuts 1999). Mother dolphin's movements tend to be relatively inefficient as well for the first few hours while the calf learns to coordinate its breathing with her (McBride and Kritzler 1951, Peddemors 1990). These problems with physical

coordination and swimming capacity arise in neonate dolphins for several reasons, including soft and unexercised swimming muscles, reduced aerobic capacity (Dolar et al. 1998, Dearoff et al. 2000, Noren and Williams 2000, Noren et al. 2000), and soft flabby fins and flukes (Tavolga and Essipian 1957, Cockcroft and Ross 1990).

Neonate dolphin calves' limited capacity for coordinated swimming and respiratory movements may be the basis for a sustained increase in swimming speed often reported for mothers following birth of the neonate (e.g., Chirigin 1987, Taylor et al. 1972). The mother's general pattern of behavior immediately following birth is to increase swimming speed and actively "place" the neonate high on her flank within a few centimeters of her body, with the calf moving down to a more lateral position ("echelon position") within a few hours (McBride and Kritzler 1951, Cockcroft and Ross 1990, Wells 1991). Increased swimming speed following parturition reportedly occurs even in mothers in captivity that had become accustomed to floating motionless (Taylor et al. 1972). These mothers abandon this rest mode after birth and begin to swim continuously at greater speeds than the other adults in the pool with the neonate in echelon position. Mothers maintain this increased and sustained swimming speed to the exclusion of stopping to take food both in captivity (e.g., Chirigin 1987, Eastcott and Dickinson 1987, Gurevich 1977) and in the wild (provisioned wild *Tursiops*, Mann and Smuts 1999).

Although increases in swimming speed for drafting mother-calf pairs after birth are apparently common, it is not likely that the increases are very great. Hydrodynamic and energetic constraints imply that speeds much over a couple of meters per second are likely too energetically expensive to maintain and may also lead to physical disruption of the drafting relationship during respiratory surfacings. This conclusion is supported by the observation that swimming speed of mother-calf pairs during the first two months after birth in wild *Tursiops* averaged about 2.4 m/sec (Mann and Smuts 1999). This speed is similar to observed average swimming speeds of 1.5-3 m/sec in dolphins swimming under normal conditions in natural environments (Table 2, Edwards 2002²).

²Edwards, E. 2002. Energetics consequences of chase by tuna purse-seiners for spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific Ocean. Southwest Fisheries Science Center Administrative Report, La Jolla, LJ-02-###, 44p., unpublished report.

The echelon swimming position characteristic of neonate dolphins involves placement of the infant within 10 cm of the mother's flank with the neonate's dorsal fin a little anterior to, even with, or slightly behind the mother's dorsal fin and the neonate's body stationed vertically somewhere between the mother's upper or mid-body (Reid et al. 1995, Mann³). The vertical position of the neonate may vary. Maintaining echelon position apparently provides a hydrodynamic "free ride" for the infant, evidenced by the relatively few fluke movements made by the infant as it "drafts" alongside its mother (e.g., Norris and Prescott 1961, McBride and Kritzler 1951, Cockcroft and Ross 1990). Although the exact hydrodynamic basis for this drafting is not known, it does appear consistent with the Bernoulli effect mechanism proposed by Kelly (1959) because the relationship appears to require sustained moderate or greater underwater swimming speed by the mother and close (within a few centimeters) association by the calf near the mother's maximum diameter. The passive nature of this drafting relationship for the calf in echelon position is illustrated by observations that calves can remain tightly associated to the mother's side even when she accelerates suddenly as in times of fright or emergency (Cockcroft and Ross 1990). Mothers in captivity have also been observed to avoid approach by other adults by accelerating into a fast swim and maneuvering the neonate to the flank opposite the other interested adult (Essapian 1953). Occasionally drafting is also observed between calves and other dolphins but the relationship tends to be short-lived. For example, an immature dolphin that was startled by an infant suddenly taking up echelon position by its' side fled around the periphery of the tank at top speed with the infant "attached" for a moment or two until the immature dolphin managed to break the drafting relationship and evade the infant (McBride and Kritzler 1951).

In addition to assisting the neonate in developing its swimming and respiratory skills, the mother's ceaseless swimming while maintaining the infant in echelon position during the first few days (e.g., Tavolga and Essapian 1957, Chirigin 1987, Eastcott and Dickinson 1987, Mann and Smuts 1999) and her strong intolerance of separations during this period (e.g., Tavolga and Essapian 1957, Cockcroft and Ross 1990) likely also provide an imprinting period similar to that which occurs among precocious locomotor young of other highly social mammals (Mann and Smuts 1999). Neonate dolphins apparently do not learn to specifically recognize their mother until some number of days after birth (Reiss 1984).

Respiration (day 1): As addressed above, the respiratory rate of neonate calves is controlled exclusively by the mother following the calf's first breath on the day of birth, and respiratory movements tend to be relatively clumsy and uncoordinated at first for both animals. The infant assumes the mother's breathing frequency while maintaining echelon position by her side. Once initiated, respirations continue both day and night with little or no diurnal variation in respiratory rate (e.g., Gurevich 1977).

Suckling (day 1): Suckling attempts usually begin within 3 or 4 hours after birth, with successful suckling becoming established within a few hours after the first attempts (e.g., Thurman and Williams 1986). During these initial suckling attempts the mother often rolls on her side to present

³Mann, J., pers.comm., Nov. 2001, University of Georgetown, Georgetown, MD, USA.

the mammary slits directly to the neonate, but this rolling behavior is soon replaced by the more normal pattern of movement by the neonate to “infant” position (e.g., Gubbins et al. 1999). Infant position involves swimming under the mother’s tail section with the neonate’s head or melon lightly touching the mother’s abdomen (e.g., Mann and Smuts 1999). In these early hours the neonate remains in infant position for only the few seconds devoted to nursing, returning immediately to echelon position afterward.

Although individual differences in suckling frequency and behavior exist and apparently are controlled by the mother (e.g., Tavalga and Essapian 1957, Triossi et al. 1998), once established, suckling in captive dolphins has been observed to continue unabated both day and night for many months (Eastcott and Dickinson 1987, Cockcroft and Ross 1990, Triossi et al. 1998). Suckling frequency is apparently highest on the day of birth and then decreases somewhat with age, although rates remain high and frequent for many months (Table 1).

Separations/Associations (day 1): During the first few hours after birth the mother does not tolerate or initiate either solitary or social separations from her infant (Mann and Smuts 1998). The only non-mother association reportedly permitted in some circumstances is tandem swimming by the mother and another well-known, usually related female wherein the two females swim with the neonate stationed between them at about the position of the adult’s dorsal fins (e.g., Tavalga and Essapian 1957).

Acoustic communication (day 1): Acoustic signaling by the calf begins immediately after birth, whenever calf separations occur ((Reiss 1984, McGowan and Reiss 1995), although under normal circumstances acoustic communication is probably relatively rare during the first few days of life because few if any separations are tolerated by the mother during this period. Acoustic signaling by the mother involves whistling to encourage her calf’s return (McBride and Kritzler 1951) and by vocalizing aggressively if the calf tries to stray against its mother’s wishes (McGowan and Reiss 1995). Similar disciplinary vocalizations have also been observed between “aunts” (non-maternal temporary caretakers) and infants (McGowan and Reiss 1995). In addition, mothers and infants tend to vocalize simultaneously during stressful events causing mother-calf separations. For example, in a group of wild but human-provisioned dolphins, both mothers and infants vocalized continually when the mothers were actively prevented by aggressive males from reuniting with their infants (Mann and Smuts 1993). Although neonate calves begin to vocalize soon after birth, it is not likely that the calf recognizes its specific mother’s acoustic communications until at least a week after birth⁴.

Summary: Birth - Day 1: During this first day the mother and calf maintain strong synchrony in movements. Probably in order to facilitate training and bonding, the mother does not forage or accept food during this period. The mother continually swims at increased speed while the physically incompetent neonate drafts in echelon position, with the exception of very brief suckling bouts. The infant begins to learn how to breath synchronously with its mother and how to suckle efficiently, although breathing movements tend to be clumsy and uncoordinated. Once initiated,

⁴Mann, J., pers.comm., Nov. 2001, University of Georgetown, Georgetown, MD, USA.

suckling is frequent and continues unabated both day and night. Under normal conditions separations are strongly avoided by the mother during this time. Calves probably are not yet capable of recognizing their mothers as distinct from other adults and may be prone to follow any large swimmer in close proximity. If separations do occur, both mother and infant tend to vocalize continuously until reunited. During this first day calves appear to be completely dependent upon their mothers for nutrition, training, protection and emotional support.

Week 1:

Swimming Activity/Position (week 1): During the first week after birth the mother-calf bond continues to be strong with almost all calf movements still strongly synchronized with the mother. During this time, life for infant dolphins appears to be concerned mainly with adjusting to aquatic life (e.g., Wells 1991) and learning to recognize the mother as distinct from other dolphins (Reiss et al. 1984). Aquatic adjustments involve learning to maintain echelon position next to the mother's flank, learning to breathe in synchrony with the mother, and improving control of suckling behavior including moving into and out of infant position.

Respiration (week 1): During this first week, dolphin calves continue to exhibit uncoordinated surfacing actions. Smooth controlled rolls through the water's surface to breathe are apparently not an innate skill for neonates. It reportedly can take up to a couple of months for this ability to develop (McBride and Kritzler 1951, Peddemors 1990) and the first few days are especially trying for the neonates. They tend to bob to the surface like corks when trying to breathe, throwing their head and much of their torso into the air and then crashing back into the water (e.g., McBride and Kritzler 1951, Peddemors 1990, Mann and Smuts 1999). The mother and calf continue to respire more or less synchronously for at least the first couple of weeks after birth (e.g., Kastelein et al. 1990, Cockcroft and Ross 1990, Amundin and Jacobsen 1999). For example, at least 70% of surfacing bouts by infants less than 3 months old were synchronized with the mother in a study of wild dolphins and all but 30 of 950 observed surfacings by neonates occurred within a meter or two of the mother, with the tightest synchrony occurring within the first week (Mann and Smuts 1999). Reported respiration rates for young dolphins vary from 1-8 breaths per minute, with most studies reporting intervals between breaths of about 30 seconds (i.e., 2 breaths per minute, Thurman and Williams 1986, Peddemors 1990, Gurevich 1977). Respiration continues to occur throughout both day and night with little day-night difference in surfacing rates (e.g., Gurevich 1977).

Suckling (week 1): Ability to achieve infant position develops very rapidly over the first day or two as the neonate first learns to successfully locate the mammary slits and then to successfully withdraw milk. The infant learns to initiate suckling by bumping the mammary area with its head just prior to suckling. During the first week the neonate spends only a few seconds at a time in this position, with the rest of the time spent in close echelon position next to the mother's flank (Gubbins et al. 1999, Mann and Smuts 1999). For example, a study of bottlenose dolphins in captivity found that probability of infant position was about 30% while probability of echelon position remained at about 70% during the first week (Gubbins et al. 1999). Suckling position was observed only 10% of the time during the first week or so in another study of captive dolphins (Taylor et al. 1972). In a study of wild dolphins, infants were observed to spend about 70% of the time in echelon position during the first month after birth (Mann and Smuts 1999).

Observed suckling rates begin to decrease somewhat by the end of this first week compared to the day of birth, although wide variation continues to exist between studies as well as between individuals within studies (Table 1). Although most of the data in Table 1 pertain to captive animals, suckling rates and patterns may be similar in wild populations given that general swimming speeds tend to be similar (i.e., about 2 m/sec) during the first few days for both wild and captive dolphins, at least under normal circumstances.

Separations/Associations (week 1): For the first week or so, the mother and calf continue to swim in close synchrony (Mann and Smuts 1999). In general, mothers reportedly won't permit separation of more than 1-2 meters during this first week (e.g., Peddemors 1990, Mann and Smuts 1998). Separations during this time tend to result from straying by the newborn and from "stealing" of the infant by other dolphins (Mann and Smuts 1998). Those few separations which do occur are quickly terminated by the mother.

Despite the mother's attempts to prevent any association with other dolphins during these first few days, occasionally other dolphins, particularly other infants and inexperienced females, may attempt to steal the infant away by "bolting" with it. This "bolting with infant" practice has been observed in both captive (e.g., Essapian 1953, Cockcroft and Ross 1990, Reid et al. 1995) and wild dolphins (Mann and Smuts 1998). Bolting occurs when another animal suddenly accelerates and swims rapidly toward and then closely alongside the mother-calf pair. This causes the infant to veer toward and take up echelon position with the bolter (Mann and Smuts 1998). For example, Mann and Smuts (1998) study of wild dolphins found that 38% of all chases by mothers during the first week were the result of bolting snatches of their infant and that the snatchers were almost all inexperienced females. This practice tends to be short-lived however, with bolting attempts rare after the first week (Mann and Smuts 1998). During these early days the mother doesn't tolerate these separations but promptly snatches the infant right back (e.g., Mann and Smuts 1998).

One reason that the bolting practice works appears to be that neonate dolphins, like many herd-forming ungulates, have a strong "follower" response for the first few days after birth (e.g. Mann and Smuts 1998) whereby neonates before they have learned to specifically identify their own mother will tend to follow whatever large moving object enters their field of view (e.g., Lent 1966, Espmark 1971, Estes and Estes 1979). Thus the success of the bolting practice during the first week may reflect the combined effects of Bernoulli hydrodynamics and a follower response in very small dolphins which have not yet learned to identify their mothers.

Observations of both wild and captive *Tursiops* indicate that by the end of the first week the mother slows her swimming speed and begins to relax her restrictions on calf separations and associations (e.g., Mann and Smuts 1998). The mother reportedly allows only brief absences at first but gradually increases her tolerance of separations and associations with other dolphins over the next few weeks (e.g., Eastcott and Dickinson 1987, Reiss 1984, Cockcroft and Ross 1990, Mann 1997, Mann and Smuts 1998, Mann and Smuts 1999). The rate at which mothers relax their restrictions on separations from their infants can apparently be affected by the mother-calf environment. For example, in a wild population regularly provisioned by humans, mother left their infants sooner (within 3-5 days rather than after the first week) and more often (Mann and Smuts 1998) than did non-provisioned mothers further offshore, implying that mother dolphins in the ETP may relax their attention to their calves somewhat more slowly than do dolphins in captivity.

Obviously, in wild populations at least, once the initial few days of ceaseless swimming has trained the calf how to maintain echelon position and to recognize its mother, the mother is going to have to leave the calf at least briefly to forage. Reported infant responses to these mother-initiated departures include 1) continuing straight ahead until retrieved by the mother or joined by another adult (Taylor et al. 1972), 2) joining other adults (usually other mature and usually related females with whom the calf is left intentionally by the mother, Taylor et al. 1972, Gurevich 1977, Mann and Smuts 1998), or 3) swimming in a small circle, vocalizing continually, in the area where the mother departed until retrieved by the mother (e.g., McBride and Kritzler 1951, Tavalga and Essapian 1957, Mann and Smuts 1998). The latter two responses are apparently common in both captive and wild situations.

Acoustic Communication (week 1): Because under normal conditions mother-calf separations are reportedly rare during the first week, acoustic communications are likely also rare. When separations do occur, the calf will probably vocalize continually until reunited with its mother. During this first week the mother is apparently also likely to vocalize repeatedly in order to encourage the calf to return to her side if the separation was not her choice (e.g., Mann and Smuts 1998). Although no study has yet shown that a calf learns to recognize its mother within the first week or at any other age, the mother's increasing tolerance of separations by the end of the first week implies that "imprinting" may be occurring during this period (Mann and Smuts 1998).

Summary: Week 1: The mother-calf association remains very strong during this period as the calf develops increasing coordination in suckling and respiratory movements and also apparently learns to identify its mother. Separations are still avoided for the most part and infants stolen away by bolting tend to be quickly retrieved by the mother. When associated, the calf remains in echelon position except for brief suckling bouts. After the first few days mothers begin to initiate some brief separations in order to resume foraging or taking food. During mother-initiated separations (e.g., when foraging), calves either tend to circle where left and whistle continuously until the mother returns, or to attach themselves to another animal if that dolphin permits it. Non-foraging-related separations continue to be strongly avoided by the mother and are still likely to elicit simultaneous acoustic signaling if they occur. Suckling remains very frequent throughout both day and night. Calves apparently continue to be completely dependent on their mothers for nutrition, training, protection and emotional support.

Weeks 2-12:

Swimming Activity/Position: These next several weeks of an infant dolphins' life are characterized by increasing physical competence and an expanding social sphere. Respiratory control and aerobic capacity increase with continual exercise and breathing practice, and suckling behaviors also become smooth and automatic. The mother increasingly relinquishes control of the infant's movements so that responsibility for continued close association between mother and calf falls increasingly to the calf.

Swimming position tends to evolve during these weeks from almost exclusively echelon to increasing periods of time in infant position. Echelon swimming predominates (70-100% of time) throughout the first month (McBride and Kritzler 1951, Reiss 1984, Mann 1997, Mann and Smuts 1999), with only about 8-10% of the time spent in infant position (Gubbins 1999, Mann and Smuts

1999) and little or no time spent socializing with other dolphins. By the second or third month infants reportedly spend about 50% of their time in echelon position, 20-50% of their time in infant position (Reid et al. 1995, Mann 1997, Gubbins et al. 1999), and about 10% of their time socializing with other dolphins (Cockcroft and Ross 1990, Reid et al. 1995, Mann and Smuts 1999).

As muscle control increases over the first 2-3 weeks the infant begins to swim farther from the mother's flank and breathes alone more often. Under normal conditions at least some infants have progressed by the end of the third week to swimming approximately a meter from their mother's flanks (i.e., not drafting), moving their flukes constantly as adults do (e.g., Cockcroft and Ross 1990). Reid et al. (1995) also report increasing mother-calf distances during the second month although the distances are not dramatic: i.e., 50-60% of the time spent in echelon position within 0.3 m of the mother, 15-40% of the time in infant position with 0.3 m of the mother, 2-8% of the time within 0.3-2m, 1% of the time within 2-5 m, and less than 1% of the time further than 5-10 m from the mother.

The mother's activity budget during the first three months in wild, non-provisioned dolphins included 50% of the time resting, 28% of the time foraging, and 19% of the time traveling (Mann and Smuts 1999). During traveling activity infants swam either in echelon or infant position (Mann and Smuts 1999).

Respiration (weeks 2-12): Respiratory movements become more efficient during this period as calf muscle mass and overall physical coordination increase. At the beginning of this period calves are still throwing their torsos out of the water with each breath but by the end of the third month calves have achieved a smooth roll through the surface to breathe (Mann and Smuts 1999). Overall, breathing synchrony with the mother decreases from approximately 100% during the early weeks (Cockcroft and Ross 1990, Peddemors 1990) to increasingly independent respiration by the end of the second month as the calf develops physical control of its respiratory movements (Mann and Smuts 1999).

Respiration rates during this period under normal circumstances reportedly vary with swimming speed. For example, respiratory rate of a captive *Tursiops* calf between 3 and 4 months of age was about 2-3 breaths/minute during periods of quiet swimming/nursing/resting, 3-4 breaths/minute during routine waking periods, and 5-6 breaths/minute during post-feeding active behaviors (Gurevich 1977). Respiratory rates also vary with age and with swimming position relative to the mother, probably as a result of increasing muscle strength and aerobic capacity. For example, under normal conditions calves reportedly need to take a breath after every suckling bout during the first day or two, but only after 2 bouts once they are about a week old and only after 5 bouts (about a two-minute period) when about 5 months old (Cockcroft and Ross 1990). Rapid increases in motor development and respiratory control after the first week are also indicated by reported improvements in many other coordinated movements, including diving, chasing, breaching, tail slapping and so forth (Reiss 1984). The infant can manage only peduncle dives during the first month or so, but by the end of about the third month is beginning to execute tail-out dives (Mann and Smuts 1999). In related observations, Cockcroft and Ross (1990) report that respiratory rate of another captive *Tursiops* calf up to about 1 month of age, breathing synchronously with its mother, was about 2 breaths/minute. When the infant began to breath independently of its mother its breathing rate increased to about 3 breaths/minute. This rate continued until about 6 months of age, when muscle development and aerobic capacity apparently increased sufficiently that breathing rate decreased again to about 2 breaths/minute.

Suckling (weeks 2-12): Suckling continues to consume a major portion of the infant's activity budget during the first three months. Suckling rates apparently continue to decrease somewhat with time although direct comparisons between studies is difficult because reported rates (and definitions of rates) vary between studies and between individuals within studies (Table 1).

Separations/Associations (weeks 2-12): Concomitant with the infant's increasing aerobic capacity and coordination during the first three months is a well-documented increase in the mother's tolerance of separations and associations by the calf with other dolphins. Whereas mothers tolerated almost no separations of more than about 2 meters during the first week, by the end of the second week mothers tolerated calf departures both alone and when with other dolphins (Mann and Smuts 1998). Infants apparently become primarily responsible for reinstating proximity during reunions, in that they approach their mothers rather than vice versa (Mann and Smuts 1998). Solitary separations were tolerated before social separations, with mothers foraging 73% of the time when infants were in solitary separation. Mothers were less likely to forage if the infant were escorted by another dolphin (only 55% of the time), and were even less likely to forage if the escort was another infant (47% of the time).

Generally by the end of the first or second month, depending on the individual personalities of both mother and infant (e.g., Chirigin 1987, Reid et al. 1995, Mann 1997) responsibility for maintaining spatial proximity apparently switches from the mother to the calf, such that the mother no longer chases the calf when the calf initiates departure (e.g., Reiss 1984, Reid et al. 1995, Mann 1997, Mann and Smuts 1998) and the calf is regularly permitted to associate with other dolphins (e.g., Eastcott and Dickinson 1987, Mann and SMuts 1998). In fact, it may fall to an adult other than the mother to return a straying calf that has not yet completely learned to return on its own (e.g., Taylor et al. 1972). For example, during the first month after birth in a population of wild *Tursiops*, mothers tolerated only 2.5 % of time spent in separations, comprising about 2 separations per hour each lasting only about 40 seconds, but during the second month mothers permitted infants to be separated from them 25% of the time, comprising about 8 separations per hour lasting about 2 minutes per separation (Mann and Smuts 1998). Distance of separation also increased, to a maximum of about 100m after three months (Mann and Smuts 1998).

Social behavior also increases during the first three months, both between the infant and its mother (e.g., Reiss 1984) and between the infant and other dolphins (e.g. Mann and Smuts 1998). For example, socializing behavior in wild *Tursiops* increased from about 3 % of the time during the first month to about 25% of the time during the second (Mann and Smuts 1998). Although the earliest associations between infants and other dolphins tend to be with other adult females likely related to the infant and mother (e.g., Tavolga and Essapian 1957, Mann and Smuts 1998), later associations tend to be with other infants and with immature or inexperienced females during play (e.g., Wells 1991, Mann and Smuts 1998). Although mothers increasingly permit more associations with other dolphins during this period, they apparently still modify their behavior to protect their infants, at least to some extent. For example, mothers in the wild reportedly tend to remain in the area rather than leaving to forage when their infants are socializing with other young (i.e., likely inexperienced) dolphins (e.g., Mann and Smuts 1998). In addition, non-mother care taking of infants by other adults tends to occur only with related and/or experienced females. For example, in a population of wild *Tursiops*, experienced females rarely escorted newborns without their mothers

and those that did escorted only related infants (Mann and Smuts 1998). Although separations and associations increase in frequency and duration during this time, the majority of the infant's time is still spent with the mother and the infant regularly returns after short excursions or play periods to respire with and rest next to or under the mother (e.g., Tavolga and Essapian 1957, Kastelein et al. 1990).

Acoustic Communication (weeks 2-12): Acoustic communication between mothers and calves during this period reflect the increasing transfer of responsibility for physical proximity from mother to calf, i.e., the calf becomes responsible for monitoring the whereabouts of the mother rather than *vice versa*. Acoustic communications between mother and calf reflect this transfer of responsibility. Mothers become more likely to be silent during voluntary separations while the infant tends to whistle continuously until reunited with its mother (e.g., Chirigin 1987, McGowan and Reiss 1995, Smolker et al. 1993, Mann 1997, Mann and Smuts 1999). Mothers reportedly tend to whistle much less frequently or not at all during voluntary separations from calves more than a couple of weeks old and may only begin to vocalize as an infant returns (e.g., Smolker et al. 1993). For example, mothers from a non-provisioned group of wild *Tursiops* were not observed to whistle during voluntary separations from their infants (SMolker et al. 1993). In contrast, the likelihood of infant vocalizations increased with distance and was virtually 100% at distances greater than about 100 meters (Smolker et al. 1993). Infant whistles seem to be directed at inducing maternal cooperation in addition to simply revealing location, and the infant whistles become individually distinct at about 4-6 months, just when the infant is beginning to separate to longer distances (Caldwell and Caldwell 1979, in Smolker et al. 1993).

Summary: Weeks 2 - 12 (Month 3): During this period dolphin calves become increasingly physically competent. Concomitantly, particularly from the first to the second month after birth, dolphin mothers increasingly transfer responsibility for maintaining close physical proximity from themselves to their calf (Mann and Smuts 1999). Drafting in echelon position decreases to about 50% of the time and synchronous respirations with the mother decrease to near zero by the end of the second month. Suckling continues to consume about 30 minutes per hour both day and night. Mothers increasingly separate for feeding excursions. Voluntary separations for socializing are increasingly initiated by both mother and calf, although calves still spend about 80% of their time within two meters of their mothers and separate for only a minute or two at a time (Mann and Smuts 1999). Acoustic communications reflect the transfer in responsibility for physical proximity from the mother to the calf. Calves' continue to signal during separations, particularly as separation distance increases, but mothers become less likely to communicate acoustically during separations. In general, calves become more physically adept but apparently remain completely dependent on their mothers for nutrition and very dependent for training, protection and emotional support.

Months 3-6:

Swimming activity/position (months 3-6): Dolphin calves reportedly remain highly dependent on and associated with their mother during this period although swimming in echelon position decreases to about 40% of the time and time in infant position increases to about 30% (Gubbins et al. 1999).

Respiration (months 3-6): During this period synchronized respirations drop to about 20%-30% of the time (Peddemors 1990, Cockcroft and Ross 1990), likely reflecting continued increases in muscle control and efficiency.

Suckling (months 3-6): Under normal circumstances, suckling continues to be an important part of a dolphin calf's daily activity although suckling bout frequency reportedly decreases slowly (Table 1).

Under abnormal circumstances, i.e., times of stress affecting the calf's emotional state, suckling frequency apparently increases, at least temporarily, so that the gradual decrease in suckling frequency with age is interrupted and the time to weaning is apparently extended. For example, a relatively steady decrease with age in suckling frequency of a captive-born *Tursiops* calf was interrupted twice by apparently stressful events: initiation of training routines at 5 months and construction noise next to the pool at 9 months (Table 2).

Separations/Associations (months 3-6): These three months are characterized by continued development of independence from the mother and by the beginning of practice foraging (e.g., Mann 1997) although separations from the mother by the calf continue to be local and brief. For example, dolphin calves up to a year of age from Shark Bay, Australia separated more than 2 meters from their mothers only about 20% of the time, with separations greater than between 5 and 20 meters occurring about 10% of the time and separations greater than 20 meters also about 10% of the time (Mann and Smuts 1999). Although individual variation occurs between infants, the average amount of time spent more than 20 meters from the mother during the first year after birth is only about 14% (Mann 1997), with individual separations rarely lasting more than a few minutes⁵.

Acoustic Communication (months 3-6): It appears likely that calves will continue to vocalize constantly during unwelcome separations from their mothers but that mothers will be increasingly unlikely to respond, at least under normal circumstances.

Summary: Months 3-6: Calves continue to develop independence in terms of breathing synchrony, associations with other dolphins, and foraging practice, but still rarely stray more than a few meters from their mothers and rarely for more than a minute or two. Dolphin calves apparently remain completely dependent on their mothers for nutrition and strongly dependent on her for training, protection, and emotional support.

Months 7 - 24:

Swimming activity/position (months 7-24): After about 6 months of age, synchronized swimming between mother and calf reportedly occurs only about 10% of the time (Peddemors 1990) but calves still spend the majority of their time with or near their mothers. For example, Gubbins et al. (1999) report that at 12 months, calves still spent about 50% of their time in close proximity to their mother, with probabilities of 30% and 35% of finding a calf in echelon or infant position, respectively.

⁵Mann, J., pers. comm. (review), 4/2002, Georgetown University, Georgetown, MD, USA

Respiration (months 7-24): During this period calves continue developing respiratory independence from their mother, with complete independence likely accomplished by the end of the period. Calf respiratory interval increases to about 2 minutes (Peddemors 1990), i.e., to about ½ breath per minute, from the 2-3 breaths/minute characteristic of earlier ages.

Suckling (months 7-24): The ability to actually catch fish develops during this period (e.g., Cockcroft and Ross 1990, Mann 1997) so suckling rates tend to decrease slowly through the months although suckling apparently continues at a relatively high rate through the end of the second year (Table 1).

Separations/Associations (months 7-24): During this period separations apparently occur commonly but remain local and brief. For example, Mann (1997) found that wild *Tursiops* infants separated more than 20 meters from their mothers only about 14% of the time during their first year, 18% during year 2, and 25% during year 3. Separations between 5 and 20 meters occurred an additional 10% of the time, with the rest of the time (75-80%) spent within 2 meters of the mother (Smolker et al. 1993). When associated, calves apparently continue to swim in infant position about 30-50% of the time through entire second year (Mann 1997). Separation durations also remain brief, with separations of 20-300m averaging about 15 minutes for six calves ranging in age from 6 months to 3.5 years (Smolker et al. 1993).

By this age dolphin calves swimming away from their mothers reportedly return immediately to her side when alarmed or frightened, at which time the mother accelerates and swims rapidly away with the calf tight to the mother's flank (Cockcroft and Ross 1990). The mother continues this alarm reaction until well over 1 year of age (Cockcroft and Ross 1990). Infant responses in any stressful situation reportedly include immediate increase in swimming speed (e.g., Gurevich 1977), direct return to echelon or infant position alongside the mother if possible (e.g., Gubbins et al. 1999) or alongside another familiar female if the mother is not available (e.g., Taylor et al. 1972) and subsequent rapid flight by both dolphins if the adult is also alarmed (e.g., Essapian 1953).

Acoustic Communication (months 7-24): As in earlier periods, it appears likely that calves will continue to vocalize during unwelcome separations from the mother, especially with increasing distance but under normal circumstances the mother will be less likely to signal in return. Under abnormal circumstance, e.g., stressful separations, it is apparently likely that both individuals will vocalize (Smolker et al. 1993).

Summary: Months 7 - 24: During this period the calf develops physical independence from its' mother in terms of ceasing to draft, learning to eat on its' own, and developing independent respiratory movements. The calf swims independently under its own power most of the time but apparently remains highly dependent on its mother. Separations occur commonly but remain local and brief, with about 75% of the time spent within 2 meters of the mother and individual separations lasting only a few minutes. The calf is likely still highly dependent on its' mother for nutrition, protection, training and emotional support well into the start of its' second year, although by the end of the second year the calf remains dependent on its' mother primarily for emotional support in times of stress.

Years 3⁺:

Swimming position/activity (years 3⁺): By the end of the second year calves reportedly spend relatively little time in echelon position but rather swim either in infant position or side by side with their mothers as adults do (e.g., Cockcroft and Ross 1990, Smolker et al. 1993).

Respiration (years 3⁺): Calf respirations are no longer dependent upon the mother's respiratory pattern, except to the extent that calves may synchronize breaths during close swimming, probably for convenience.

Suckling (years 3⁺): By the end of the third year dolphin calves are apparently foraging independently (e.g., Perrin et al. 1976; *Stenella attenuata* weaning age in ETP approx. 1 year) although (bottlenose) calves reportedly continue to nurse, "at least occasionally for the entire period of infant swimming, typically 3-6 years and occasionally up to 8 years" (Mann et al. 2000).

Separations/associations (years 3⁺): Although calves apparently have outgrown the majority of physical dependence upon the mother by the end of the second year, the mother-calf bond remains close. For example, wild *Tursiops* calves 1-4 years old in Shark Bay, Australia still spend 30-45% of their time in infant position with their mother (Mann and Smuts 1999) and spend about 75% of their time within 2 meters of their mother (Smolker et al. 1993). Mothers and calves through year 4 remained within 5-20 meters of each other about 10% of the time and separated more than 20 meters only about 15-20% of the time (Smolker et al. 1993). In addition, calves as old as 6 years reunite with their mothers during times of fear or stress (e.g., Essipian 1953, Gowan and Reiss 1995). Although infants are in some ways precocious at birth, they apparently remain highly socially dependent upon their mothers for several years in the wild (e.g., Smolker et al. 1993).

Acoustic Communication (years 3⁺): As the calf matures and becomes increasingly independent from its mother acoustic signaling will likely decrease during separations, although under normal circumstances likelihood of calf vocalizations apparently continues to increase with distance from the mother through at least the first three years (Smolker et al. 1993). Presumably during times of stress calves (and perhaps mothers) would revert to earlier stages of constant acoustic signaling during separations.

Summary: Year 3⁺: From the third year on swimming and respiration apparently become fully independent activities for calves and suckling has been replaced by independent feeding. Although it appears that dolphin calves are essentially independent of their mothers by this time in terms of physical support, dolphin calves apparently continue to maintain close physical association with her many years, apparently for emotional support and perhaps training. Despite their increased physical independence, calves continue to return immediately to their mothers in times of stress.

II. Chase and Encirclement Procedure

Chase and encirclement involves searching for and locating (detecting) a likely school of dolphins (i.e., one that appears to be associated with enough tuna to be worth making a set),

initiating chase by launching a number of speedboats from the seiner, and encircling the dolphins by maneuvering them into the closing purse seine. Each of these stages of chase are examined in greater detail below with respect to characteristics that may affect the activities of mothers and calves as described in previous sections.

Detection: Dolphin schools may be detected by one of several means (hand-held binoculars, very large mounted binoculars, bird radar, bird flocks, or helicopter-mounted searchers) but the first indicator to a dolphin school that a seiner is in the area is likely the seiner's helicopter or the sound of the seiner's engines. Schools may or may not react to the helicopter but they invariably react to either the sound of the purse-seiner's engines (if in a regularly-fished area) or to the sound of the speedboats when these aluminum craft with large outboard engines slide off the back deck of the seiner and set off at full speed to overtake the dolphin school and slow it down sufficiently that the purse-seine can be set around it.

Chase: The chase itself is not linear but tends to be more curvilinear, similar to the tactics sheepdogs or cattle dogs use to herd a group of animals to a particular spot desired by the master, with the herding individual taking position on the side of the school (or herd) opposite the desired endpoint. The objective of the chase is to overtake the school on the side away from the vessel and then to move the speedboats in such a way that the forward end of the dolphin school curves toward the seiner and eventually takes the whole school (or some preselected part) within the closing arc of the seine. While the net is being closed around the school the speedboats move in small tight circles within the closing mouth of the net to prevent the dolphins from swimming out and taking the tuna with the before the net is fully closed. Thus the chase persists until the school can be turned, slowed and "corralled" within the seine. Chase time, defined as time from speedboat launch to the time the net enters the water, tends to last about 30 minutes (spotted dolphins, Myrick and Perkins 1995).

Encirclement: The speedboats continue their activities until the net is closed, circling between the closing ends of the net and thus preventing the dolphin's escape. Encirclement time, defined as time from net entry into the water to full closure of the net, tends to last about another 40 minutes (spotted dolphins, Myrick and Perkins 1995).

III. Likely Behavioral Responses to Chase

The first part of this section summarizes the likely behavioral response of ETP dolphin *schools* to the presence of tuna purse-seiners, based on review of existing information on dolphin school reactions to perceived threats. The second part discusses potential behavioral responses of mother dolphins, and the concluding part discusses potential behavioral reactions of calves from birth through about two years of age. The calf sections include suggestions about the likelihood of mortality following permanent separation from the mother for that particular age.

Dolphin school fright reactions: Becoming aware of an approaching or overflying helicopter and or approaching speedboats apparently elicits a typical dolphin school fright reaction, i.e., the school coalesces, speeds up, and tries to evade the helicopter and/or speedboats and seiner (e.g., Au and Perryman 1982, Hewitt 1987). These responses are similar to dolphin school fright reactions

reported from other areas including observations from both captive and wild groups. In captivity, reported dolphin group responses to general threat stressors, e.g., to a shark being introduced into the tank, included immediate schooling and loud whistling (e.g., Essapian 1953). Wild dolphins reportedly tend to respond to threats in one of two ways, depending on the stressor type. Stressors sensed first at a distance reportedly elicit a cohesive group response while stressors perceived as an immediate and instantaneous threat elicit independent responses of increased swimming speed and evasive behavior by individuals.

Regardless of threat type, all threat responses involve rapid swimming and avoidance of the threat (e.g., Belkovich 1991). For example, Taylor et al. (1972) report that the appearance of sharks resulted in coordinated avoidance by schools of wild dolphins such that the dolphin schools swam under or split to swim around the sharks. Playing of killer whale sounds, where the threat could not be seen and likely not localized, led to rapid swimming in tight formation. When a threat occurred instantaneously, such as a gunshot or inadvertent hooking by a fisherman, the school's coordinated movements broke down and dolphins tended to flee individually as rapidly as possible such that the stronger individuals rapidly outdistanced the slower or less mobile individuals which were soon left behind. Reports of ETP dolphin behavior in response to first sensing a seiner appear to be consistent with the first type of response, i.e., in response to a distant perceived threat individuals move close together, increase speed, and attempt to avoid the threat.

Mother Responses: If ETP dolphin mothers react to threat in a manner similar to mothers in other herd-forming mammals (e.g., ungulates), which is ecologically likely, then they will be more likely to focus on maintaining proximity to other associated adults rather than accommodating their calves.

The reported tendency for mother dolphins to begin by the second week to transfer responsibility for maintaining proximity to their calves strengthens the likelihood that mother dolphins may respond more strongly to other nearby adults than to their calves. Due to the diminished physical capacity and stamina of calves relative to their mothers, it appears likely that mothers in cow-calf pairs during chase will have to choose between remaining with their calf or remaining with the rest of the adults in the school, at least until the calves have gained the ability to keep up with the school on their own. The actual likelihood that a particular mother dolphin will separate from her calf probably varies with individual characteristics such as specific personality traits, prior maternal experience, prior experience with chases, and physical capacity, as well as with the individual characteristics of a particular chase. For example, it is common for calf mortality to be higher among inexperienced (first-time) mothers (e.g., Tavalga and Essapian 1957, Sweeney 1987). Presumably separations might be less likely for more experienced mothers less likely to panic, and for shorter chases at slower speeds but more likely for more stress-prone mothers during longer, faster chases. In general, the responses reported to date imply that separation due to maternal behavior is more rather than less likely under many circumstances.

Because mother dolphins apparently take more responsibility for maintaining proximity with their calf during the day of birth and perhaps for the week or so after, the mother during this time may be more likely than when the calf is older, to alter her behavioral priorities in favor of remaining with the calf rather than remaining with the school. At least in captivity, mothers around the time of birth sometimes distance themselves from the other dolphins in the pool, and work to keep their infants separated from other dolphins for the first few days. If this tendency to behavioral isolation occurs in the wild, then a mother with a newborn calf might be more likely to separate from

the rest of the school despite the presence of a chase in the area. However, separating in this way makes little ecological sense in a pelagic population where protection from predators depends primarily on association with other dolphins. Thus in the wild situation of the ETP the more ecologically prudent choice for mother dolphins is to remain with the other adults in the fleeing school.

After the first week or two, as mother dolphins increasingly transfer responsibility for maintaining physical proximity to their calves, it appears to be increasingly likely that mother dolphins will focus their efforts on remaining associated with other adults during the chase. The herd-forming behavior of ETP dolphins coupled with the reported propensity for mother dolphins to let responsibility for association rest with the calf implies that maintaining proximity to the rest of the school will take precedence over remaining with the calf, for many mothers during many chases.

Thus until calves are old (large and strong) enough to keep up with the rest of the school, it appears more likely that calves will tend to be left behind than that mothers will tend to leave the school to accommodate their calves. The observed calf deficit in dolphin mortality indicates that at least some mothers do become permanently separated from their calves during chase. Consideration of the potential interplay between adult fright reactions and calf physical inabilities leads to a reasonable conceptual mechanism by which the observed calf deficit might arise.

Calf Responses: In general, it appears that calves will likely try to the best of their capabilities to remain associated with their mothers during chase at least for the first 5 or 6 years of age, although it also appears likely that most calves will lack the physical capacity to do so for at least the first year or two after birth. Likely age- and activity-specific responses of calves to chase are discussed below, in chronological order.

Birth-Day 1:

Swimming activity/position (day 1): Newborn calves, influenced by the “follower response”, will likely attempt to remain closely associated with their mothers, or at least some large dolphin, at all times including during chase. However, the lack of muscle strength, aerobic capacity, stamina and coordination reported in newborn dolphins would prevent a neonate from swimming as fast as its mother under its own power during chase for more than a few seconds, if even that long. Under normal (non-chase) circumstances neonate dolphins apparently overcome their inability to swim with coordination or strength by drafting next to their mothers so that the larger dolphin provides the power required to move the neonate through the water and also the coordination for an efficient respiratory interval. Unfortunately, sustained swimming speeds under chase conditions are higher than under normal circumstances (3-4 m/second versus about 2 m/second, Table 2 in Edwards 2002⁶). These higher speeds probably destroy the mother-calf drafting relationship due to a combination of two factors, 1) the change in respiratory behavior exhibited by dolphins during increased sustained swimming speeds characteristic of response to chase by tuna vessel speedboats,

⁶Edwards, E. 2002. Energetics consequences of chase by tuna purse-seiners for spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific Ocean. Southwest Fisheries Center Administrative Report LJ-02-29, unpublished report.

and 2) the huge mass difference between neonates and their much larger mothers (Table 3). At the relatively slow speeds typical of most observed drafting the mother dolphin's breathing behavior involves a partial roll through the surface exposing only a portion of each animals' back for a brief period. Because the swimming speed is relatively slow, this partial exposure of the back is apparently sufficient to expose the blowhole long enough to accomplish a full exhalation/inhalation.

At faster speeds a full breath likely could not be accomplished in time if only a portion of the back was exposed; in addition, faster speeds create much increased hydrodynamic drag. The combination of these two factors probably causes the observed surfacing behavior of ETP dolphins during chase, in which the dolphins exit the water totally in low flat leaps with each breath such that they travel several meters through the air before reentering the water (e.g., Au et al. 1988). Any drafting relationship will be completely disrupted by this breathing method because drafting apparently depends on the pressure field of the water between and around the mother-calf pair. As soon as the mother leaves the water, the calf will immediately begin to fall behind, both because of the smaller momentum associated with its smaller size and because it will still be traveling through (dense, high friction) water while its mother is traveling through (less dense, lower friction) air.

To make matters worse, if the drafting relationship is maintained until just as the mother leaves the water, i.e., to just at or below the surface, then the neonate will be left in the especially high-drag portion of the water column, which will contribute to even greater slowing⁷. While the neonate is left in the water, the mother will sail through the air to reenter the water at least a couple of meters ahead of the calf and moving at a much higher velocity. In addition, during the first hours and days after birth, dolphin calf respiratory movements are clumsy at best so that trying to manage a sufficient respiration under these circumstances is also likely to be a problem for the calf. Then, in order for the drafting relationship to be reestablished (at least until the next breath), the mother would have to voluntarily slow her speed until the neonate could catch up, if in fact the baby was capable of such directed swimming so soon after birth. But slowing her speed would cause the mother to fall away from the rest of the school, which presumably was her impetus to swim fast in the first place.

In the absence of a drafting relationship with its mother, a newborn calf will likely attempt to establish a new drafting relationship with any other large nearby dolphin given the "follower response" combined with the apparent inability of newborn dolphins to recognize their specific mothers until a few days after birth. If the other dolphin is swimming fast then a new drafting relationship could likely be established, but again only until the larger dolphin sails out of the water to take its first breath.

Thus it appears likely that at least some newborn dolphins will be left to swim under their own power during chase. Because it is apparently impossible for newborn dolphins to swim even at non-chase speeds under their own power, it appears very unlikely that they could remain with the rest of the school for more than a few seconds. Unless the mother remains with newborn, it appears quite likely that the infant will soon be left alone.

⁷Hydrodynamic drag is about 5 times greater at the surface compared to drag at least three body diameters submerged (Hertel 1966).

Respiration (day 1): As with swimming position, the effect of chase on respiratory behavior of mother-calf pairs will depend on the mother's reaction to the fishing operation, given the calf's limited and inefficient behavioral repertoire during these early days. If the mother ignores the chase and continues normal behaviors with her calf, then the chase would be irrelevant to the pair. If the mother increases swimming speed and changes her breathing pattern, she will no longer be able to help with the neonate's respiratory behavior and the calf will have to rely on its' own devices until such time as the mother might return after chase. While the calf may be able to respire adequately on the day of birth without its' mother help, the process will be relatively inefficient and likely be increasingly tiring, further reducing any energy reserves the calf may have in this first hours after birth.

Suckling (day 1): Regardless of the mother's reaction to chase, it seems likely that suckling will be interrupted for at least some period of time. If the mother swims with the school and leaves her calf behind, obviously suckling will be interrupted during her absence, if in fact she returns later. Given the nearly constant suckling characteristic of neonate dolphins, the loss of energy supply for even a few hours, particularly combined with increased energy costs of unassisted swimming and respiration, could be expected to significantly decrease the calf's survival odds. If the mother does not return at all then the calf's energy supply will most likely be cut off completely (see Section IV: Potential for Adoption).

Separations/Associations (day 1). During the day of birth and first few days after, a neonate dolphin apparently does not specifically recognize its mother. While a neonate would likely try to reestablish close swimming position with another adult as soon as possible if it became separated from its mother, it would not necessarily choose only its mother. If the mother is not nearby, this might expose the neonate to aggression by other adults, particularly males and unrelated females. Regardless of the adult chosen, it appears very unlikely that a close physical association could be maintained with any adult during chase, or that neonate calves could identify their specific mother during or after chase.

Acoustics (day 1): Given the reported habit of neonate and young dolphins to whistle and circle where left during a separation, it seems unlikely that the presence of an undefended, noisy calf would go unnoticed for long by predators such as sharks. Sharks are frequently present during sets on dolphins by tuna vessels and shark predation on dolphins is well known (e.g., Leatherwood 1972, Connor and Heithaus 1996).

Summary: Birth-Day 1: Although it appears likely that neonate calves will make every effort to remain associated with their mothers during chase it also appears likely that mother-calf pairs on the day of birth will become separated if a chase occurs, due to a combination of school-seeking behavior by the mother, physical disruption of the drafting relationship, and physical incompetence of the calf. Although likelihood of physical separation may be affected by specific maternal experience and personality, and by characteristics of individual chases, separation appears more likely than not in most cases. It does not appear likely, should a calf become separated from its mother during the day of birth, that the calf could survive for more than a few hours alone and not

for longer periods unless reunited with its mother (whom the calf is unable to recognize) or adopted by a lactating female, which appears to be highly unlikely (see Section IV: Potential for Adoption).

The likelihood of reunion after the chase, should the mother survive, may also be quite low during the first day after birth, depending on the distance of separation, continuing noise and confusion after the dolphins are released (obscuring any vocalizations made by mother and/or neonate⁸) and the neonates' inability to recognize its own mother.

Week 1. Because no great changes in behavior, physical prowess or body size occur during this period, comments from the previous section pertain to this period as well. Although dolphin calves apparently learn to identify their mother specifically by the end of this first week, this ability is not likely to affect likelihood of separation. Separation still appears very likely in most cases unless the mother alters her typical fright behavior in order to remain with her calf.

Summary: Week 1: As before, survival for more than a few hours in the absence of the mother appears unlikely due to the likelihood of both predation and death by starvation. Likelihood of reunion with the mother after chase also appears to remain low, at least for noisy chases of relatively long duration, despite the calves likely ability to acoustically recognize its mother, because reunion will be dependent on the mother relocating the calf rather than vice versa.

Weeks 2-12: Although calf swimming, respiratory, and suckling abilities become increasingly refined and efficient during this period, the continued disparity in size between the mother and her calf (Table 3) will likely continue to interfere with maintenance of drafting during sustained high speed swimming during chase and with the ability of a calf to keep up with the school under its own relatively limited power. The likelihood of separation appears to remain high if the mother does not alter her behavior to accommodate her calf. Based on reports from mother-calf pairs under normal (i.e., non-chase) conditions, it appears increasingly unlikely as the calf grows larger and more competent that the mother will alter her normal fright adult behavior in response to chase, so that the likelihood of separation will continue to be high. It remains likely that these small calves will not be able to maintain school speeds for more than a few seconds or perhaps a minute or two, so that once again if the mother does not remain with the calf, the calf will likely be left alone. It also appears likely that the calf's acoustic response to separation will remain the same, i.e., constant signaling, and that adoption will not occur.

Summary: Weeks 2 - 12: Even if predation could be avoided, it continues to appear unlikely that a lone calf could survive for more than a few hours to perhaps a few days for the larger calves before succumbing starvation.

⁸Mann, J. pers.comm. (review), 4/2002, Georgetown Univ., Georgetown, MD, USA.

Month 3-6. During this period the amount of time spent drafting reportedly decreases significantly under normal (i.e., non-chase) circumstances, probably due to the increasing size of the calf, although calves reportedly return to the drafting position when swimming fast (e.g., towards a large fish school)⁹. While this sort of short-term drafting may be sustainable for the few seconds involved in accelerating toward a fish school, it is still not likely to be sustainable for the duration of a typical tuna-vessel chase. In addition, the increasing size of the calf will create a significant energetic burden for the mother¹⁰. As swimming ability increases with increased muscle coordination, strength, and mass, the calf will become increasingly responsible for providing the power to remain associated with its mother. At the later stages of this period it might begin to be possible for a calf to achieve school speeds for some limited period of time (a minute or two¹¹), so that separation from its mother might be somewhat less likely even if the mother did display the typical adult fright reaction, at least for chases of limited speed and duration. Given the still relatively small size (Table 3) and aerobic capacity of calves at this age, it appears that separation is still likely and will increase with chase duration and speed. In addition, it appears likely that acoustic signaling will continue during separations.

Summary: Month 3-6: Given dolphin calves' continued small size, acoustic signaling on separation, and dependence upon milk at this age, it still does not appear likely that a lone calf in this age group would survive permanent separation from its mother for more than a few days before succumbing to predation or starvation.

Month 7 - Month 24: During the early part of this period dolphin calves are apparently still primarily dependent on milk, are still relatively small with limited physical reserves, and will likely have difficulty remaining with the school during a chase. By the end of the first year (month 12) calves are still relatively small (Table 3) but are beginning to outgrow their complete dependence on milk and presumably have somewhat greater physical stamina. By the end of the second year calves will be approaching adult size (about 80% adult length, Table 3), are apparently weaned and feeding

⁹Mann, J. pers. comm (review), 4/2002, Georgetown University, Georgetown, MD, USA

¹⁰Edwards, E. 2002. Energetics consequences of chase by tuna purse-seiners for spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific Ocean. Southwest Fisheries Center Administrative Report LJ-02-29, unpublished report.

¹¹*ibid.*

independently (Perrin et al. 1976) and their physical size and prowess may now allow them to maintain speed with the adults in the school, at least briefly (perhaps a minute or two¹²) during short and/or relatively slow chases. Although the physical dependence of the calves on their mothers decreases significantly during this period their emotional dependence apparently continues. Calves continue to spend most of their time in close physical proximity to their mothers and reunite with their mothers immediately during times of stress. Acoustic signaling by calves apparently decreases so that signaling during separation occurs mostly during times of perceived stress and forced separation from the mother, but this would likely include chase-induced separations.

Summary: Month 7 - Month 24: Survival probability of lone calves is probably quite low during the early part of this period but may be relatively high by the end of the second year when calves apparently have achieved physiological independence from the mother and reasonably capable swimming capacity. Calves are still likely to become separated from the school during chases with higher speeds and longer durations, and are still likely to succumb to predation if not reunited with their mothers or other adults within a few hours. Starvation is also still likely, at least for the younger calves, if not reunited with their mothers within a few days.

Year 3⁺: As dolphin calves approach and achieve adult size and stamina the likelihood of separation as well as the likelihood of mortality should separation occur should progressively decrease to adult levels. By the end of the third year, likelihood of survival in the absence of the mother is probably quite high.

Summary: Birth - Year 3⁺: Existing information on behavior of dolphin mothers and calves implies strongly that likelihood of survival for separated calves not reunited with their mothers is extremely low during the first year, low during the second year, moderate during the third year and quite high from year 4 onward.

IV. Potential for Adoption

¹²*ibid.*

The possibility that mothers and calves may be permanently separated as a result of chase and encirclement, either because the mother was captured and killed while her infant survived or because some other event prevented their reunion, raises the question of whether orphaned infants could continue to survive without their mother's swimming assistance, milk, or protection. Theoretically this would be possible if the infant could find alternative sources until the infant was old enough to be independent. Obviously, the older the infant at separation the more likely its survival.

However, although several records exist of adoptions or attempted adoptions of dolphin infants by other dolphins (e.g., Thurman and Williams 1986, Kastelein et al. 1990, McBride and Kritzler 1951, Ridgway et al. 1995) there are several factors which imply that successful adoptions are not likely to occur in the ETP on a regular basis. In particular, the circumstances under which successful adoptions tend to occur in dolphins are apparently fairly restrictive and are less likely to be found in wild than in captive situations (e.g., Packer et al. 1992). Because dolphins produce and nurse only one calf at a time, they are unaccustomed to and do not permit nursing by more than one infant at a time. They also give total preference to their own offspring. The only circumstances under which mature female dolphins have been observed to permit non-offspring nursing has been 1) *in captivity* within a few weeks prior to parturition, in which case the non-offspring was rejected upon birth of the female's own infant (e.g., McBride and Kritzler 1951), 2) *in captivity* during and after induction of lactation by previously non-lactating females (Ridgway et al. 1995), and 3) *in captivity* by lactating females after loss of their own calf (e.g., Smolders 1988). Two observations have been reported of young dolphins being associated with an adult of another species in the wild¹³ but in both instances observations were very limited and did not provide any evidence for the duration or extent (i.e., lactation permitted or not) of the associations.

In *captive* situations it is not uncommon for other females to attempt to steal a newborn calf (e.g., Thurman and Williams 1986) or for mothers or foster mothers to isolate themselves and their neonates from other individuals to prevent such stealing (e.g., Kastelein et al. 1990). However, in *wild* situations it does not appear likely that a neonate would survive being stolen (or permanently separated from its mother due to some circumstance related to chase and encirclement) unless it was stolen (or adopted by) by a lactating female, and that apparently would not happen unless the lactating female had already lost her own calf. While it is common to observe mothers apparently being assisted in infant care giving by other females both in captivity and in the wild (e.g., Tavolga and Essapian 1957, Mann 1997, Mann and Smuts 1998, Mann and Smuts 1999), these are generally other females without infants of their own and therefore would be non-lactating and unable to support an orphaned infant. In wild populations adoption by a lactating female prior to parturition would most likely be at best a temporary solution lasting only until the mother gave birth to her genetically-related offspring and subsequently rejected the orphaned calf. A calf in the wild probably also would not survive an induced lactation because even if the female were willing because it took over two weeks of supplemental feeding before the induced females in captivity produced enough milk to support the calves; even then the milk was of low fat content (nutritionally unsatisfactory) for several more weeks thereafter (Ridgway et al. 1995).

¹³Perrin, W. 2002, SWFSC, La Jolla, CA, pers. comm.

Adoption of a separated calf in the wild by a lactating female which had lost her own calf is possible but appears to be unlikely, based on an extensive review of non-offspring nursing in a variety of mammals (Packer et al. 1992). Packer (1992) found that non-offspring nursing was more likely 1) in captivity, and 2) in mammals which produce large litters. It was least likely to happen in wild populations of mammals that produce single offspring. When non-offspring nursing did occur in species which give birth to single young, it was more common in species where infants steal milk and where mothers continue to lactate after losing their young. In general, non-offspring nursing is rare in monogamous species and tends to involve continued nursing after losing one's own young. The rarity of non-offspring nursing, especially in the wild, is likely due to the selective disadvantage for the mother of delaying reproduction of her next genetically-related offspring, while continuing to sustain the increased energy costs of lactation for the benefit of another's offspring (Packer et al. 1992).

Although under many circumstances adoption may not be a common event, it is possible that the unusual circumstance of chase and encirclement in the ETP might create a chase-induced disruption of multiple cow-calf pairs, which in turn might lead to higher than normal probability that an orphaned calf might find a lactating female whose own calf had been permanently lost. However, even if adoptions may be occurring at a higher than normal rate, it will only be occurring due to a higher than normal availability of lactating females that have recently lost their own calf, because simultaneous nursing of two or more calves apparently is not permitted by lactating dolphins. That is, in order for a calf to be adopted, the adopting mother must have recently lost her own calf and the orphaned calf must have recently lost its mother. Thus, a lactating female dolphin killed in a purse-seine net whose calf was not yet independent will likely represent an unobserved calf mortality one way or another, either mortality of her own calf if not successfully adopted, or unobserved mortality of the adopting mother's original calf, which might or might not be chase-related. Thus, the possibility of adoption, even if it were unexpectedly common, would not provide a mechanism for reducing or eliminating calf mortality associated with death of lactating females in purse-seine nets because some other calf will have to die in order for the newly orphaned calf to be adopted.

SUMMARY AND CONCLUSIONS

Based on this review of existing literature, it appears that behavioral characteristics of mothers and physical characteristics of calves likely contribute to separation during chase by tuna purse-seiners in the ETP, with the likelihood of separation being particularly high at birth and decreasing *slowly* with age. Especially during their first few months dolphin calves apparently have little coordination, muscle strength, or aerobic capacity, and few social skills. In addition, after the first week or so responsibility for remaining associated apparently falls increasingly to the calf while the mother responds primarily as an unencumbered adult. The likelihood that permanent separation from the mother will lead to mortality (e.g., when the mother has been killed in the set) appears to be especially high for dolphin calves still dependent on milk, due to behavioral factors including relatively low probability of adoption and increased predation risk incurred by their likely habit of vocalizing during separation.

Likelihood of separation during chase of a particular mother-calf pair is probably affected by prior experience, physical capacity, and personality of both mother and calf, as well as by chase duration and speed. However, while individual variations doubtless exist in behavior and physical

abilities of individual mothers and calves, the information reviewed here implies strongly that at least some calves are likely to become permanently separated from their mothers during chase at least some of the time. The information also implies strongly that the younger the calf, the more likely that permanent separation will lead to subsequent unobserved mortality, with mortality especially likely for calves less than about two years of age.

ACKNOWLEDGMENTS

This manuscript was significantly improved by comments from Janet Mann, Steve Reilly, Bill Perrin, and other reviewers, for which I am very grateful.

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Table 1. Reported dolphin calf suckling rates of various types.

Suckling Events/hour	Age	Citation
4-17	first week, less with age	Reid et al (1995)
2	first 2 weeks, less with age	McBride and Kritzler (1951)
5-10	through month 1	Cockcroft and Ross (1990)
2-3	first 7 weeks	Eastcott and Dickinson (1987)
10-20	first few weeks	Wells (1991)
2-8	weeks 2-9, less with age	Reid et al. (1995)
2-6	to 3 months, less with age	Peddemors (1990)
Suckling Bouts/hour		
6	day of birth	Peddemors et al. (1992)
2-4	during week 1	Reid et al. (1995)
1-3	weeks 2-9, less with age	Reid et al. (1995)
1-2	after 2 months	Peddemors (1992)
4	through 3 months	Gurevich (1997)
3-4	six months and older	Gurevich (1997)
0.5	by the end of year 2	Peddemors (1990)
Suckling Bout Duration (Seconds)		
17-24	up to 1 month	Kastelein et al. (1990)
9-10	first 7 weeks	Eastcott and Dickinson (1987)
6	through 8 weeks	Triossi et al. (1998)
7-10	average through week 9	Reid et al. (1995)
7-10	through 3 months	Gurevich (1997)
4-5	9-52 weeks	Triossi et al. (1998)
3-4	through 30 months	Peddemors (1990)
4-10	6 months and older	Gurevich (1997)
Suckling Minutes/hour		
20-40	through month 3	Cockcroft and Ross (1990)
20	through year 2	Cockcroft and Ross (1990)

Table 2. Effects of disturbance (training at 5 months, construction noise at 9 month) on suckling rates of a captive *Tursiops* calf (Peddemors 1990).

Suckling Events/day	Age
40	5 months, undisturbed
45	5.5 months, disturbed
38	6 months, undisturbed
30	9 month, undisturbed
38	9.5 months, disturbed
30	10 months, undisturbed

Table 3. Approximate size at age for *Stenella attenuata* in the eastern tropical Pacific Ocean (Perrin et al 1976, Hohn and Hammond 19##).

AGE	TOTAL LENGTH (cm)	WEIGHT (kg)
Birth	85	6.5
7 days	87	7
1 month	90	8
3 months	98	10
6 months	110	14
1 year	129	22
2 years	154	38
adult female	190	70

APPENDIX - Response to Reviewer Comments

April 19, 2002

Prepared by Elizabeth Edwards, 4/19/02.

Responses to Reviewer's Comments on CIE -S12 "Potential effects of chase and encirclement on behavior and energetics of spotted dolphin (*Stenella attenuata*) mother-calf pairs in the ETP" and CIE-S13 "Energetic Consequences of chase by tuna purse seiners for spotted dolphins in the ETP" both by Elizabeth F. Edwards.

1. Response to comments from De. Guise:

Pages 4-5: "Reviews...seem unrealistic in view of field observations that calves do remain with cows during chase and capture operations". Verbage has been added at to CIE-S12 various places in the manuscript pointing out that probability of separation of specific mother-calf pairs will be affected by behavioral and physical characteristics of the individuals involved as well as by characteristics of individual chases (i.e., speed and duration) .

Page 16: "interesting and relevant...but quite pessimistic...". The reviewer is incorrect in saying that aerial observations "concluded that cow-calf pairs are not usually separated during chases".. Aerial photographs show a few seconds of swimming sequence of a given school. Persistence of a calf with a cow outside of those few seconds has not been demonstrated. The comments summarized above address the issue the reviewer raises again here.

2. Response to comments from D. Martineau:

pg 24-25: reviewer requests more emphasis on importance of frequent suckling to support energy needs of very young calf. Comments to that effect added in sections pertaining to very young calves.

3. No comments received from G. Bossart or R. Ortiz.

4. Response to comments received from J. Mann:
Appendix A. Responses to CIE reviewers.

Prepared by Elizabeth F. Edwards:

Responses to Reviewer's Comments on CIE -S12 "Potential effects of chase and encirclement on behavior and energetics of spotted dolphin (*Stenella attenuata*) mother-calf pairs in the ETP" and CIE-S13 "Energetic Consequences of chase by tuna purse seiners for spotted dolphins in the ETP" both by Elizabeth F. Edwards.

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3. No comments received from G. Bossart.

4. No comments received from R. Ortiz.

5. Response to comments received from J. Mann:

pg 8: review of CIE-12: reviewer comments that “some of the cited literature needs to be reviewed more carefully”. Review of references identified numerous instances of citations to a 1999 paper confused with a 1997 paper. These have been corrected. No other suggestions for corrections were made for this paper.

pg 9: review of CIE-13: The only direct suggestion for additional work appears in paragraph 2, recommending assessment of the likelihood that calves older than three months of age might still draft during times of stress. This cannot be determined from the existing literature, but would require either collection of new data, or possibly, examination of existing aerial photographs of ETP dolphin schools evading vessels and/or helicopters in the ETP. However, aerial photographs tend to capture only a few seconds in the swimming history of school, so the persistence of drafting by older calves probably couldn't be established from those data.